

study into the mauve stinger. “The trouble is that we know so little about jellyfish,” says Haughton. Most people think of them as having little impact on ecosystems. “Now we need to learn, very quickly, about their behaviour and about their breeding patterns in our waters.”

The team is getting its first basic data by monitoring the number of jellyfish spotted from the decks of ferries crossing the Irish Sea. This will be followed by work on research vessels in the coming months trawling for jellyfish in a careful pattern to determine the numbers and distribution of the jellyfish.

The researchers hope to gather the basic data needed to predict whether last year's jellyfish bloom, which was unprecedented in size in these waters, is likely to occur again in the near future.

Meanwhile, Spanish authorities are already working out the best way of protecting beaches from the expected appearance of the mauve stinger. They cannot simply be netted, as this would also trap other marine organisms because they can sink to depths of several metres. And if the fragile creatures are damaged, detached tentacles maintain their poison for some time and can themselves drift in towards beaches. The best measure so far has been to send flotillas of small boats offshore to scoop up jellyfish at the surface using small nets.

The Spanish environment minister, Cristina Narbona, admits more effort is needed. Researchers believe that a year-round programme of monitoring needs to continue and propose a list of specific measures: to station jellyfish hunting boats at beaches under threat; to provide local people and tourists with information on how to protect themselves; and to close beaches to bathers when necessary.

But more essential, they say, is the global ecological crisis highlighted by the proliferation of jellyfish and to change the way fisheries are managed worldwide.

Nigel Williams

Quick guides

Audience effects

Klaus Zuberbühler

What are audience effects? Social beings ranging from humans to cockroaches are affected by the presence of others. In the animal literature, the term ‘audience effect’ has been used specifically to refer to changes in the signalling behaviour of individuals caused by the mere presence of other individuals.

Why are audience effects interesting? An important question in animal communication is whether signals are targeted at particular receivers or whether they are just signs of arousal. If an animal alters a signal in the presence of an audience, then it becomes possible that the signal is emitted strategically, perhaps based on the signaller's assessment of how a receiver might be affected.

When were audience effects first described in animals? Male domestic chickens produce specific calls when finding food and conspecifics often respond by approaching the caller. Many animals produce specific vocalisations when discovering food, but such behaviour has often been disregarded as uninteresting manifestations of arousal. A series of studies led by Peter Marler, however, has provided empirical evidence that male chickens do not always give food calls when discovering food, but do so preferentially in the presence of hens, sometimes even if no food is present.

How widespread are audience effects? Audience effects are probably widespread in animal communication, although surprisingly little research has addressed the problem directly. Empirical studies have been conducted with primates and birds, but interesting results have also been obtained in fish and insects.

How did audience effects evolve? There is good evidence across taxa that bystanders attend to and can learn from observing social interactions between conspecifics.

Primates, birds, and even fish can infer a social dominance hierarchy by simply watching the outcome of conflicts. Another important context is paternal behaviour. In species where males provide paternal care, females sometimes base mate choice decisions on a male's parental skills, and males seem to advertise these in the presence of females. The more general point is that natural selection will favour signallers that are able to adjust signal production to maximise their own benefit, and taking into account the presence, composition, and attention of their audience is an important component in this process. Interesting examples come from Siamese fighting fish: males who have lost a contest with another male spend less time displaying to a female who has witnessed the fight compared to naïve females, as if these males are taking into account future mating probabilities, which is determined by the females' observations.

What are the current research questions? Some authors use the term ‘audience’ in a relatively loose sense, often interchangeably with ‘receiver’. In these studies, communication is investigated as a dyadic interaction between a signaller and a receiver, and the focus is on how different features of the receiver — reproductive value, social position, or focus of attention — impact on signaller behaviour.

In the wild, acts of communication are rarely purely dyadic processes. Signalling usually occurs within a network of animals in which individuals are socially connected to each other. Many vocal signals, particularly those given in alarm and agonistic contexts, transmit over large distances much beyond the immediate receivers, suggesting that they have been selected to function in networks with large and invisible audiences. Audience effects, defined in this more strict sense, refer to triadic situations that involve a signaller, a receiver and an untargeted bystander, and the main question is how bystanders affect the signalling interactions between the two individuals.

One pivotal question in audience effect research concerns the cognitive processes available to the communicating individuals. This is a difficult problem and no experiment is powerful enough to provide conclusive

answers. In one study, macaque monkey mothers were exposed to a predator but, somewhat surprisingly, they did not attempt to alert ignorant offspring (the audience) more than knowledgeable ones. More recent research has shown, somewhat contrastingly, that male Thomas langurs do not stop giving alarm calls when threatened by a predator, until every single group member has responded with at least one alarm call. These males appear to monitor the vocal behaviour of each group member and perhaps keep track of who has and who has not responded with alarm calls, an unparalleled example of an audience effect based on complex cognition.

Are primates special? Researchers interested in the evolution of the mind have traditionally preferred to work with primates. Are audience effects the result of hardwired response predispositions, or are they the product of a flexible insightful mind? Evidence for the latter is perhaps most compelling for ape gesture studies. These studies have shown that apes carefully adjust the production mode of their signals depending on the attention state of the targeted receiver. For example, before using visual gestures, chimpanzees position themselves such that they have visual contact with the receiver, or they use tactile or acoustic gestures if the receiver is socially engaged elsewhere. In the vocal domain, various primates adjust call rates depending on who is in the audience, particularly mates, genetic relatives, or competitors. For example, female vervet monkeys alarm-call significantly more when with their own offspring compared to unrelated juveniles.

In the triadic sense, audience effects have recently been described in free-ranging chimpanzees. Victims of aggression tend to exaggerate the severity of aggression experienced by modifying the acoustic structure of their screams, but only if the audience consists of individuals who are capable of intervening and helping the victim (that is, if someone in the audience is equal or higher ranking than the aggressor). Apes, and possibly other primates, thus go much beyond assessing their audience in terms of biologically important categories, and also take into account psychological variables, such as

attention, capacity to help, or ability to comprehend.

Have audience effects been observed in humans? Social psychology has long been interested in how people's performance is affected by the presence of others. For example, individuals usually perform better with easy or well-learned tasks in the presence of an audience, while the opposite is the case for difficult or poorly learned tasks. Another good example for a dyadic audience effect is infant-directed speech ('motherese') during which speakers produce distinct prosodic contours when interacting with a non-linguistic receiver, usually a baby or a pet, to convey intentions such as prohibition, approval, or attention. An example for a triadic audience effect is 'code switching' by which two individuals change from one language or dialect to another to express solidarity or exclude others from conversations. Although both effects are based on the knowledge state of the audience, these examples also illustrate that the behaviour of these signallers is not necessarily based on conscious rational decisions.

What's next? With regards to signallers, research on audience effects has shown that animals from a wide range of taxa can take into account the nature of their audience when producing a signal. These effects are probably widespread in animal communication, but many groups of animals have not been investigated. One prediction is that audience effects are more likely to have evolved in social species.

For most non-primate animals, it is largely unclear if audience effects are the result of hardwired evolutionary predispositions, an understanding of receiver behaviour, or an explicit intent to actively inform. The evidence is somewhat better for primates, but a thorough understanding of the cognitive mechanisms underlying audience effects is still of primary interest.

With regards to the audience, evidence suggests that bystanders are not merely inadvertent interceptors, but actively evaluate signalling interactions and relate them to their social consequences. A largely unresolved problem is exactly how and when bystanders exert their

influence on signallers. There is evidence that audience effects take place before the actual act of communication: signallers and receivers appear to already know that they are being watched when starting a signalling interaction. The cognitive or physiological mechanisms responsible for these effects are largely unknown.

Many studies have investigated audience effects in dyadic interactions, in which the targeted receiver also acts as the audience. For reasons outlined earlier, a fruitful future direction to investigate audience effects is the triadic setting, which more closely approximates natural communication and ensures results that are ecologically and evolutionarily relevant.

Finally, audience effects raise some interesting questions with regards to evolutionary theory. Are signallers adjusting signal output in order to enhance their reputation in a social group through image scoring? Empirical work will need to test whether signalling behaviour is advantageous in this way, and whether bystanders have evolved abilities to detect deceitful image scorers.

Where can I find out more?

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School of Psychology, University of St Andrews, Scotland, UK.
E-mail: kz3@st-andrews.ac.uk